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BRAYA IN COLORADO

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The discovery of a population of *Braya* in the high mountains of central Colorado in 1950 by Messrs. H. D. Ripley and R. C. Barneby is not only of interest but several problems arise as a result of it. This station is nearly a thousand miles south of the nearest known locality for the genus *Braya* in Alberta.[1] The Colorado plants are closely related to a wide-ranging and polymorphic arctic and subarctic species, *B. humilis*, which has often been placed in the genus *Torularia*. Abbe (1948) retained it in *Braya*, but more recently Böcher (1950), in a thorough cytotaxonomic study of Greenland material, chose to treat the species as a *Torularia*. To properly handle the Colorado plants, two problems need to be dealt with: (1) Are they one of the many isolated and distinctive populations of *Braya humilis*, or are they a distinct species? (2) Do they (and *B. humilis*) belong to the genus *Braya*, or should they be placed in *Torularia?* I shall attempt to answer the last question first.

Torularia would appear to have been originally founded upon *Sisymbrium* (*Braya*) *humile* (Schulz, 1922). However, one finds that Schulz, in this first published work using the name *Torularia* in generic rank, merely made a new combination without providing a generic description. The generic name *Torularia* was first validly published in Das Pflanzenreich (Schulz, 1924) and the genus was based on species formerly referred to subgeneric divisions in *Sisymbrium* and *Malcolmia*. *Torularia* was used as a sectional name in *Sisymbrium* by Cosson (1885) to contain the single species *S. torulosum*. Schulz raised Cosson's sectional

[1] This ignores the transfer by Jones (1929) of *Draba graminea* to *Braya*. Actually the species is unquestionably a *Draba*.

name to generic rank. From this, it follows that *Torularia torulosa* is the type species and becomes the point of reference for the generic name *Torularia*. When one considers the relationships of *Torularia*, using *T. torulosa* as a principal point of reference, it is prefectly clear that this genus as a whole is much more closely related to *Malcolmia* than it is to *Braya*. Furthermore, considerable stretching is needed to include *Braya humilis* in it. On the other hand, *B. humilis* has often been confused with *B. linearis*, which in turn was at one time included in *B. alpina*, the generic type species of *Braya*. The pattern of characteristics observable in *B. alpina* applies also in a general way to *B. linearis* and *B. humilis*. On morphological grounds, there is no sound reason for excluding *B. humilis* from the genus *Braya*. The latter is an older name than *Torularia* and takes precedence in any circumstance where the two are in direct competition.

Chromosome Numbers in Braya

Chromosome numbers so far reported for *Braya* are: *B. alpina*, 2n = 32 (Manton, 1932); *B. linearis*, 2n = 64 and *B. purpurascens*, 2n = 64 (Löve and Löve, 1948); *B. linearis*, n = 21, 2n = 42, and *B. humilis* (as *Torularia*) 2n = 56 (Böcher and Larsen, 1950). A collection of *B. humilis*[2] from Alaska (Drury, no. 3298) has 2n = 40. The Colorado population (Rollins, Weber, and Livingston, no. 5153) was counted from buds fixed in the field and was found to have n = 32. In studying fuelgen preparations of root tips of the Alaskan collection, Drury 3298, a great range in chromosome size within the compliment was noted. Some of the smallest chromosomes are about the same size as one arm of a medianly constricted large chromosome. Such small chromosomes could easily be mistaken for one arm of a large chromosome or, as was most often the case, one arm of a large chromosome was mistaken for a small chromosome. The tendency was to count more rather than fewer chromosomes in figures where there was any possibility of confusion. It was only after a close study of numerous preparations that 2n = 40 was established as a certainty for this collection.

From the above counts, polyploidy in the genus is seen to be well established. Thus one of the mechanisms having a direct

[2] I am indebted to Dr. L. O. Gaiser for the accompanying cytological data.

bearing on speciation and upon the expected variation within species has been demonstrated. Although it is not known whether apomixis occurs in the genus, it may not be amiss to point out that apomixis combined with polyploidy could easily account for the distinct but only slightly different populations of *B. humilis* so clearly indicated by Abbe (l. c.). All counts fit a polyploid pattern except those of n = 21 and 2n = 42 for *B. linearis* made by Böcher and Larsen. In high polyploids, the loss or gain of a few chromosomes is apparently easy and may affect the morphology and physiology of a particular race very little or none at all. It would be surprising to me if some aneuploidy did not occur in a genus such as *Braya*, where polyploidy is obviously so wide spread. However, further work is needed to fully clarify this apparent discrepancy of 2n = 42 and 2n = 64 in the same species. The discovery of 2n = 40 in an Alaskan population of *B. humilis* and of n = 32 in the Colorado population of *B. humilis*, subsp. *ventosa*, further ties this species into *Braya* and points against removing it to *Torularia.*

Braya humilis

Three different chromosome counts from as widely separated areas as Alaska, Colorado, and Greenland, representing the extremes in the range of *B. humilis* in North America, call for an explanation. It would be ideal to obtain many more counts from intermediately situated populations to determine the over all pattern for the species, but that is at present impossible. I have turned to pollen measurements to see whether there is any correlation between pollen size and chromosome number.

The pollen of *Braya humilis* is tricolpate with the longest axis considerably exceeding the shortest. In shape, the grains are probably *perprolate,* using the terminology of Erdtman (1952). The exine is prominently reticulately pitted and in this respect the different pollen samples studies were relatively uniform. Measurements were made from the extremities on both the long and short axes, including the exine. Ten grains of each sample were measured except in one instance where two size-classes were found, where ten of each size-class were measured.

The lowest chromosome number, 2n = 40, was found in Alaska material, *Drury, no. 3298.* Pollen of this same collection measured 32.1 × 19.1 μ (ave. of ten grains). In another Alaskan collection, *Drury, no. 2131*, filled grains averaged 30.5 × 20.5 μ. In this latter collection, non-filled (and non-staining) grains measured 22.5 × 15.1 μ. Nearly fifty per cent of the grains were in the latter class. Preparations showing both size-classes of grains undisturbed within the anthers were prepared in order to make certain there was no contamination involved. Unfortunately, pollen from the same collection used by Böcher (l. c.) to obtain chromosome counts was not readily available. However, *Braya humilis* is of restricted occurrence in western Greenland and the plants sampled are likely to be the same taxon as those from which chromosome counts were obtained. Pollen from a collection by *M. P. and A. E. Porsild, s. n.*, Aug. 4, 1914, averaged 33.0 × 19.4 μ. The pollen of the Colorado population averaged 36.7 × 20.0 μ. Thus it is seen that there is a rough correlation between pollen size and chromosome number, the Alaskan plants with $2n = 40$ having pollen 32.1 × 19.1 μ; the western Greenland plants with $2n = 56$ having pollen 33 × 19.4; and the Colorado plants with $2n = 64$ having pollen 36.7 × 20. Other pollen measurements on American material were within the same general range—a collection from eastern Greenland, *Sørensen 4230*, referred to subsp. *arctica* by Böcher, having 31.6 × 18.6 μ; a collection from Anticosti Island, *Marie-Victorin and Roland Germain* 27–203, having 32.2 × 19.6 μ; and a collection from Fort Churchill, *Gillett 2242*, having 34.4 × 21.8 μ. However, a collection from southwestern Kansu, *J. F. Rock 12269*, has pollen somewhat smaller than that of the smallest of the American collections. The grains average 26.7 × 16.3 μ. Generalizations cannot safely be made on such meagre data, but there is an indication that lower chromosome numbers are to be expected in the Asiatic populations. This points to Asia as the area of origin for *Braya humilis*. As the species spread eastward through Alaska, polyploidization increased the chromosome number, so that the highest ploidy is found, so far as is known, at the greatest distances from its area of origin. Such assumptions as to the origin and spread of *B. humilis* are supported also by morphological details, there being a closer resemblance between Alaskan and Altai plants than between Altai plants and those from more remote stations in North America.

Both microcytes and giant pollen grains were found in a number of collections. The presence of unusually small or large grains is an indication of meiotic irregularity, particularly an ultimate unequal distribution of the chromosomes. These abnormalties are frequently associated with polyploidy and are most likely to occur in unbalanced polyploids, such as triploids, pentaploids, etc. Their persistence is often permitted in a given species by the presence of asexual reproduction. It is perhaps significant that in one of the Alaskan collections studied (*Drury, 2131*), there were two size-classes of pollen grains, as indicated above. The smaller unfilled grains represented nearly fifty per cent of the total. This is a strong indication of meiotic irregularity. The presence of such a high percentage of sterile grains may be taken as evidence that a high degree of fertility is not required for the survival of these particular plants. From this it may be inferred that some form of apomixis probably permits the circumvention of the usual sexual process. It is unfortunate that seeds were not available from this particular collection so that such a hypothesis could be tested.

Polyploidy coupled with apomictic reproduction would explain very neatly the genetic origin and maintenance of the divergent relatively uniform isolated populations found in *B. humilis* today. Unfortunately, we have only circumstantial evidence of apomixis being present. There is no proof at this time. On the other hand, polyploidy has been definitely shown in a comparison of populations from three widely separated areas and pollen studies indicate that an even wider range in chromosome numbers is probably present.

I am in agreement with Böcher (l. c.) that the time for preparing a comprehensive cytotaxonomic treatment of the *Braya humilis* complex has not yet arrived. Although there is room for much work on the American plants, the most serious impediment is our lack of information about the Asiatic plants belonging to this complex. After examining the specimens from Asia in the Gray Herbarium and comparing them with the plate in Ledebour's Icones (1830), and then checking them against Meyer's (1831) amplified description, I am not fully convinced that typical *B. humilis* occurs in North America. It has been commonly assumed that this was the case, but proof is not obtainable from the limited Asiatic material at my disposal. At the present time, it is not at all certain whether we must treat *B. humilis* as a large polymorphic species with many distinctive local populations, or whether some of these may not actually represent distinct localized species.

In attempting to see what the relationships of the Colorado plants are to the various races of *B. humilis*, as described by Abbe (l. c.), it was soon evident that they do not belong to any of these six geographically localized populations. Nor do they agree in morphological details with northwestern North American material commonly placed in *B. humilis*. The nearest approach to any *Braya* is to Abbe's race 4 from Table Mountain in Newfoundland. The Colorado material falls within *B. humilis* if it is accepted as a wide-ranging polymorphic species as in Abbe's treatment. However, the plants are more distinctive than most of the races described by him. Since they about parallel the divergence found by Böcher in the north and east Greenland plants which prompted him to establish subsp. *arctica*, it seems appropriate to designate the Colorado population as a subspecies of *B. humilis*.

Braya humilis (C. A. Meyer) Robinson, subsp. **ventosa** subsp. nov. Herba perennis caespitosa; caulibus decumbentibus vel erectis 3–6 cm. longis; siliquis divaricatis 1.5–2 cm. longis, ca. 1 mm. latis.

Perennial, usually with an unbranched caudex; basal rosette well developed; stems several to numerous, pubescent with 2- to 3-pronged trichomes; basal leaves numerous, thickened, spatulate, entire or with a few teeth, sparsely pubescent with branched trichomes, 1–2 cm. long, 2–3 mm. wide; cauline leaves 1–3, petiolate, spatulate; inflorescence dense; infructescence much elongated, often occupying nearly the entire stem; petals white; sepals more or less persistent; pedicels stout, 1.5–3 mm. long; siliques divaricate, slightly curved, pubescent with mostly bifurcate trichomes, 1.5–2 cm. long, about 1 mm. wide; styles ca. 1 mm. long.

Type in the Gray Herbarium, collected on rocky slopes of eastern extension of North Star Mountain, 1.5 miles west of Hoosier Pass, border of Park and Summit Counties, Colorado, Aug. 7, 1951, *Reed C. Rollins and William A. Weber 51288*. Other collections seen: same location (in flower) July 7, 1951, *Reed C. Rollins, William A. Weber, and Charles Livingston 5153* (GH); same location, July 11, 1950, *H. D. Ripley and R. C. Barneby 10393* (GH).

Subspecies *ventosa* is definitely perennial with a well-developed taproot. The outer stems are prostrate or decumbent but the inner are mostly erect. Nearly the entire stem is occupied by the elongated infructescence, the lower pedicels being subtended by leaf-like bracts. The sepals are quite persistent, remaining attached in many instances where the silique is fully mature. In this latter respect, subsp. *ventosa* is closer to *B. linearis* than it is to *B. humilis*.

The Colorado population was studied on two occasions in the summer of 1951. Both times I was accompanied in the field by Dr. William A. Weber of the University of Colorado and, on the first trip, also by Mr. Charles Livingston. On the first visit, we had great difficulty finding the population because of the small size of the plants and their tendency to grow nearly concealed by rocks or other plants. Had we not been given the most precise directions as to the exact location by Mr. Barneby, I am sure we would not have found it. The plants grow on a fairly steep rocky slope with a rather sparse covering of other tundra species. It is possible, of course, that other stations for *B. humilis*, subsp. *ventosa* will be discovered but it must be extremely localized in its occurrence or it would surely have been collected earlier.

In order to bring the nomenclature into conformity with our conclusions as to the generic disposition of *B. humilis*, the following new combination is required:

B. humilis (C. A. Meyer) Robinson, subsp. **arctica** (Böcher) comb. nov. Based upon *Torularia humilis*, subsp. *arctica* Böcher. Medd. om Grønl. Bd. 147. no. 7, p. 29.

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A FLORISTIC STUDY OF COOK COUNTY, NORTHEASTERN MINNESOTA

Fred K. Butters and Ernst C. Abbe

(*Continued*)

TYPHACEAE

Typha latifolia L. Seagull Lake, BA 941; Swamp (?) Lake, "L.W.K." 1; Schroeder, BA 1085.—Shallow pools and ditches; very local.

SPARGANIACEAE

Sparganium americanum Nutt. Sawbill Creek, Bg 117; Loon Lake, BR 6517; Pope Lake, L. W. Krefting 10; Cascade River, C. B. Reif A19.—Streams; locally abundant.

S. chlorocarpum Rydb. Royal River, BsH 258.—Sluggish stream.

S. chlorocarpum, var. acaule (Beeby) Fernald, Rhodora **24:** 29. Cross River, BR 6377.—In mud at edge of river.

S. angustifolium Michx. Partridge Lake, BA 792; "Bearskin Lake," U. S. F. S. (Aug. 28, 1935).

S. fluctuans (Morong) Robins. Sawbill Lake, Bg 118; Rove Lake, BBsH 105.—Locally abundant; BBsH 105 was growing in 5 ft. of water in a small pond.

S. minimum (Hartm.) Fries. Grand Portage, BA 967.—Shallow pools at edge of cedar swamp.

ZOSTERACEAE

Potamogeton Robbinsii Oakes. Northern Lights Lake, U. S. F. S. 43.

P. zosteriformis Fernald, Mem. Gray Herb., III, p. 36, 1932. Devil's Track River, U. S. F. S. 34; "Superior Forest," "A. H." (no date, s. n.).

P. foliosus Raf., var. macellus Fern. "Bearskin Lake," U. S. F. S. (Aug. 28, 1935).

P. Berchtoldi Fieber (typical). Seagull River, BA 901; East Pope Lake, "L. W. K." 13; Birch Lake, BA 805b.

P. Spirillus Tuckerm. Cross River, BR 6373; Birch Lake, BA 805.

P. epihydrus Raf., var. typicus Fernald, Mem. Gray Herb. III, p. 114. 1932. Swamp Lake, "L. W. K." 6; Devil's Track Lake, U. S. F. S. 36.—The submersed leaves are somewhat under 0.5 cm. in width, but the plants otherwise correspond to var. *typicus*.